Evolutionary Relationships of Stromatolite-Building Cyanobacteria

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Stromatolites are one of the most abundant fossils in Precambrian rocks, and as such, provide valuable information about Earth's earliest biosphere. The microfossil record in stromatolites traces Earth's history since the oldest life over 3.5 billion years ago. Modern stromatolite structures are formed by sediment trapping and/or mineral precipitation of microbial mat communities living in shallow-water environments. Microbial mats are "living" stromatolites—modern-day analogs that provide an opportunity to study the way ancient microbial communities lived and evolved. Though direct evidence is lacking, fossil stromatolite diversity appears to be under the direct influence of microbial species diversity. Most modern microbial mats are constructed by cyanobacteria, but this may not have been the case for the earliest fossil stromatolites. Oxygenic photosynthesis first evolved in the cyanobacteria, so understanding the relationship between cyanobacterial and stromatolite morphology is crucial to determining the biotype of these early stromatolites and the timing of this crucial evolutionary event.

This study focuses on a type of modern coniform stromatolite constructed in the thermal springs of Yellowstone National Park by a fine filamentous cyanobacterium called *Phormidium*. These mats are considered the best analog for the fossil conophytons that are one of the most distinctive groups of Precambrian stromatolites, with a fossil record dating back to 3.5 billion years. A variety of stable organic compounds, generally referred to as "chemical fossils" or "biomarkers," have been extracted from these coniform mats, in particular the 2-methylhopanoids. The 2-methylhopanoids are considered a biomarker for the cyanobacteria, and detection of its fossil equivalent in 2.7-billion-year-old sedimentary rocks has established a minimum age for the evolution of oxygenic photosynthesis. Understanding the relationships among the source of this important biomarker, stromatolite morphology, and cyanobacterial biodiversity provides essential clues in deciphering the identity of the original mat-building community and establishing the antiquity of *Phormidium* conophyton stromatolites.

A variety of morphologically similar *Phormidium* stromatolites have been isolated from the Yellowstone coniform mats. They form three distinct groups based on lipid biomarker composition. Two of the *Phormidium* groups synthesize hopanoids, but only one of these, represented by *Phormidium* OSS, synthesizes the cyanobacterial specific 2-methylhopanoids. The third group, represented by *Phormidium* RCO, synthesizes no hopanoids. A variety of molecular tools (denaturing gradient gel electrophoresis, DNA sequencing, and molecular phylogenetics) have been used to characterize the evolutionary relationship among these coniform-mat, *Phormidium* isolates. Phylogenetic analysis supports the three groups based on lipid biomarker composition (figure 1). Further, the cyanobacteria isolated thus far form a monophyletic group, indicating a single origin. This moderately thermophilic, coniform *Phormidium* clade is as well supported as several other well-established cyanobacterial clusters such as the *Microcystis* or halotolerant *Euhalothece*. Such close phylogenetic relatedness suggests a common evolutionary path within a close microbial community, giving rise to coniform biodiversity.

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